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ABSTRACT

Visual recognition, navigation, tracking, and imagery are posited to involve some of the same types of representations and processes. The first part of this paper develops a theory of some of the shared types of representations and processing modules. The theory is developed in light of neurophysiological and neuroanatomical data from non-human primates, computational constraints, and behavioral data from human subjects. In developing theories of some of the high-level computations that are performed by the visual system, three problems which must be solved by any visual system are considered: (1) position variability; (2) figure/ground segregation; and (3) non-rigid transformations. The second part of the paper develops a mechanism for the development of lateralization of visual function in the brain. The theory rests on a set of relatively simple, uncontroversial properties of the brain, including: (1) processing components; (2) exercise; (3) selectivity; (4) "central" bilateral control; and (5) reciprocal innervation. This theory leads to predictions about the lateralization of the putative processing modules. The third part of the paper examines critical tests of these predictions, and reviews relevant empirical findings in the literature. Eight pages of references and several figures are included. (Author/LMO)

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Visual Hemispheric Specialization: A Computational Theory

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Visual Hemispheric Specialization:

A Computational Theory

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Abstract

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Visual Hemispheric Specialization:
A Computational Theory

There has been great interest in how the two cerebral hemispheres are specialized for visual processing since the time of John Hughlings Jackson, who in 1874 reported an apparent right-hemisphere specialization for recognition. Theories of visual specialization, following the fashion in the field of neuropsychology, have tended to focus on various dichotomies; for example, the right hemisphere has been said to be specialized for information about global shape and the left specialized for information about details (see Springer and Deutsch, 1981). This strategy, of trying to discover a dimension that will capture the differences in processing, has much to recommend it. Indeed, if there are general principles that distinguish types of processing systems, then those systems should be able to be characterized in terms of sets of such dimensions. However, the dimensions that have been explored to date have not been closely related to theories of processing systems, and have generally not been well motivated. Rather, the dimensions chosen typically are selected on the basis of intuition and apparent descriptive power.

In this paper I present an alternative way of attempting to understand visual hemispheric specialization. This approach is based on the idea of "natural computation" (see Marr, 1982), in which we try to understand the brain in terms of components that interpret and transform data in various ways. The theory we develop here focuses on "high level" visual processes, which can be characterized as those processes that can be directly altered by one's

knowledge and beliefs. (Thus, although one may believe that a bright light will occur and so close one's eyelids, retinal processing is not considered "high level" because it is not directly altered by the belief.) We focus on this class of processing primarily because there is no evidence that low-level, sensory visual processing is lateralized (e.g., see Berkley, Kitterle, and Watkins, 1975; Di Lollo, 1981; Rijsdijk, Kroon, and Van der Wildt, 1980).

On this characterization, then, high level visual processing is involved in visual recognition, navigation, tracking, and mental imagery. We are particularly interested in how experience can play a role in the organization of such visual functions in the two cerebral hemispheres. In developing this theory we will make use of neurophysiological and neuroanatomical data from non-human primates, computational constraints, and behavioral data from human subjects. We begin by considering what vision and imagery are for, and derive computational constraints from this analysis.

I. VISUAL PERCEPTION AND VISUAL IMAGERY

Before beginning to formulate a theory of how a function might be carried out by the brain, it is useful to begin by considering the purpose (or purposes) of that function. Vision has two primary purposes: First, we try to recognize objects and parts thereof. This function allows us to apply previously gained knowledge to newly encountered objects. For example, once one has recognized something as an apple, one knows that it is edible, has seeds inside, and so on. In order to carry out this function, visual input must be encoded in such a way that it makes contact with the appropriate previously stored information (see Marr, 1982). Second, we use vision to navigate though space (and not bump into objects or walk into holes) and to

track moving objects (avoiding or intercepting them, as is appropriate). In these cases, the goal is not to encode information in order to access relevant memory representations. Rather, the goal is to compute metric spatial relationships and to update them as objects move relative to one another.

It is interesting that the purposes of imagery parallel those of vision. Perhaps this is not surprising, given that virtually all definitions or characterizations of imagery hinge on its its similarity to like-modality perception. For example, visual imagery is usually characterized as "the experience of seeing in the absence of the appropriate sensory input" or the like. Indeed, having an image produces the conscious experience of "seeing", but with the "mind's eye" rather than with real ones. [FOOTNOTE 1] One purpose of imagery uses recognition to make explict information stored implicitly in memory. That is, we encode patterns without classifying them in all possible ways; indeed, there may be an infinite number of ways to classify a shape (e.g., relative lengths along all possible pairs of axes). In order to make explicit a particular aspect of a remembered pattern, we may form an image and "internally recognize" that aspect of it. That is, we "recognize" parts and properties of imaged objects we had not previously considered. For example, consider how you answer the following questions: What shape are a beagle's ears? Which is darker green, a Christmas tree or a frozen pea? Which is bigger, a tennis ball or an orange? Most people claim that they visualize the objects and "look" at them in order to answer these questions (and the behavioral data support this claim; see Kosslyn, 1980). Imagery is most often used in memory retrieval when the to-be-remembered information is a subtle visual property that has not been explicitly considered previously and cannot

be easily deduced from other facts (e.g., information about the category in general; see Kosslyn and Jolicoeur,, 1980).

A second purpose of visual imagery parallels the perceptual mapping and tracking functions of perception. Imagery is a way of anticipating what would happen if we were to move in a particular way or if something else is moving relative to us. That is, we use imagery to perform "mental simulations," looking to "see" what would happen in the analogous physical situation. For example, we might imagine a jar and "see" if there is room for it at a given spot on the refrigerator shelf, or we might mentally project an object's trajectory, "seeing" where it will hit. Imagery is used here when one reasons about visual appearances of objects under transformation, especially when subtle visual relations are involved.

Finally, we can use our imagery abilities in the service of more abstract thinking and learning. Shepard and Cooper (1982) review numerous cases of scientific problem-solving in which "imaged models" were used as aids to reasoning. Einstein, for example, claimed that his first insight into relativity theory arose when he considered what he "saw" when he imaged chasing after and matching the speed of a beam of light. However, these kinds of uses of imagery seem to rely on the first two uses of imagery: In visual thinking and learning, we use imagery as a way of retrieving tacit knowledge from memory or as a way of performing mental simulations.

Given the apparent parallels between the purposes of imagery and vision, it is not surprising that much empirical research has demonstrated that imagery and like-modality perception utilize some common processing mechanisms (for reviews see Finke, 1980; Finke and Shepard, in press; Kosslyn, 1980, 1983;

Shepard and Cooper, 1982). For example, if one is holding in mind a visual image (e.g., of a flower), this will impair visual perception more than it impairs auditory perception, but vice versa if one is holding in mind an auditory image (e.g., the sound of a telephone ringing; see Segal, 1971). Perhaps most interesting, manipulating objects in images reveals time-courses like those observed in the real world. For example, Figure 1 illustrates pairs of stimuli used in a classic study by Shepard and Metzler (1971). They asked subjects to decide if the objects were the same or different shape, irrespective of their orientation. Figure 2 presents the results, indicating a highly linear increase in decision time as more mental rotation was required to bring the forms into congruence. This result is impressive because images are not actual, rigid objects, and hence are not constrained by physics to have to pass through intermediate positions when the orientation of an imaged object is changed. Similar results are obtained with image scanning. Kosslyn, Ball and Reiser (1978) asked subjects to close their eyes and imagine the map illustrated in Figure 3. This map had seven locations, which were positioned so that there were 21 distinct inter-location distances between all possible pairs. The subjects began by "focusing" on a given location on the imagined map (e.g., the tree), and then decided whether a second named location was or was not on the map (e.g., the hut versus a bench); they were asked to respond in the affirmative only after they had the second object clearly in focus. As is evident in Figure 4, increasingly more time was required to scan between pairs of locations that were increasingly farther apart on the map, indicating that an imaged map can "stand in" for the actual one. Kosslyn (1975) reports another finding that is especially suggestive: If an object is imagined at a

small size, more time is required to "see" its parts than if the object is imagined at a larger size (see Kosslyn, 1980, 1983). This result is intriguing because it suggests that objects in images are subject to spatial summation, a well-known property of neural mechanisms used in vision.

INSERT FIGURES 1, 2, 3, 4 ABOUT HERE

Three Problems in Vision

Although the behavioral phenonena reveal that imagery and like-modality perception share underlying mechanisms, they do not provide much illumination on the nature of those mechanisms. However, such data become very useful when we consider them in combination with neuropsychological findings and computational theorizing. Indeed, behavioral and neuropsychological data are especially useful in guiding one to formulate what Marr (1982) called a "theory of the computation." That is, a computation can be regarded as a "black box that transforms input in a systematic, informationally-interpretable way. A theory of a computation specifies what must be computed and why. Such a theory justifies positing a given computation by an analysis of what problems must be solved and the requirements on the solution to those problems. The goal of a computation is specified, as well as the nature of the input and constraints on the solution. This sort of theory is to be distinguished from a "theory of the algorithm," which specifies the specific steps actually used to carry out a computation. The theory of the computation is a fundamental step, outlining the basic "processing components" that should be included in the theory; the

theory of the algorithm fleshes out the details of how the computations are performed. In this paper we will concentrate on the first level, focusing on a theory of the computations used in one aspect of imagery.

We can use the inference that imagery shares mechanisms with perception to discover a remarkable amount about the structure of the information processing system underlying high-level vision. We do so by first considering some fundamental problems that must be solved by a visual system. Our brains have apparently solved these problems in specific ways, and the outlines of these solutions are now apparent in the literature on the neurophysiology and neuroanatomy of visual perception; these solutions have direct implications for a theory of visual processing.

Thus, in this section we will begin to develop theories of some of the high-level computations that are performed by the visual system. We will do so by considering three problems which must be solved by any visual system and the apparent solutions to these problems adopted by primate brains. In the following section we will explore the implications of these inferences for a theory of imagery, assuming that visual imagery makes use of visual processing mechanisms.

1. <u>The Problem of Position Variability.</u>

The same object is likely to occur at various positions in the visual field. Nevertheless, once we have seen an object, we can recognize it just as easily when it subsequently is in a different position in the field. Logically, there are two ways we could perform this feat: On the one hand, when an object is encoded initially, the visual system could associate a separate representation with each of the possible positions of the object.

This is one interpretation of the mechanism suggested by McClelland and Rumelhart (1981) in their theory of word perception. They associate a representation of each letter with each position in the field. (This was done so that the same letter could be detected in more than one position in a word.) On the other hand, when an object is encoded initially, it could be stored using representations that are associated with a set of positions in the field. In the limit, only one representation would be used for all positions. This is the solution Marr (1982) offered for the position variability problem; Marr suggested that the appearance of objects is stored in "object-centered" representations. In such representations, the locations of parts of objects are specified relative to other parts, not to positions in space.

The solution adopted by primate visual systems to the problem of position variability is now evident in the neurophysiological literature: It has been found in primates that visual cells in area TE (near the anterior end of the inferior temporal lobe) have very large receptive fields, and respond when patterns are present over a wide range of positions (the receptive field sizes are usually larger than 20 x 20 degrees of visual angle). This area of the brain has been shown to be critically involved in recognition per se (see Mishkin, 1982). Thus, the primate's solution to the position variability problem relies on not representing the position of a pattern in the high-level shape representation system. (Incidentally, this is a good example of how facts about the neurological underpinnings of behavior can have direct bearing on theories of cognition; this finding is a significant challenge to the McClelland and Rumelhart model.)

One implication of this solution is that only one shape can be

recognized at a time (although we could rapidly switch back and forth between stimuli, only one would be processed at any given instant); if multiple stimuli were being processed simultaneously, the large receptive fields would often result in the system's not being able to tell if there is one stimulus or two of the same stimuli being presented in different locations (e.g., the letter A in a word). Hence, figure/ground segregation is necessary to isolate individual patterns before they can be processed further. If this is done, then duplicate patterns can be isolated and processed separately, preventing confusions about how many of a pattern are present in the field.

However, we do know where an object is when we see it. Thus, there must be a separate representation of an object's location, which implies two separate mechanisms--one to represent a shape independently of its position and one to represent its position. And in fact, Ungerleider and Mishkin (1982a) summarize evidence for "two cortical visual systems." Their claim is that the ventral system, running from area OC (primary visual cortex) through TEO down to TE, is concerned with analyzing what an object is, whereas the dorsal system, running almost directly from circumstriate area OB to OA and then to PG (in the parietal lobe) is concerned with analyzing where an object is. Figure 5 illustrates the relevant areas of the primate brain.

INSERT FIGURE 5 ABOUT HERE

Two sorts of data are relevant to Ungerleider and Mishkin's claim. First, the neuroanatomy and neurophysiology support this distinction. There are well-known neural connections running along both pathways, and the visual

properties of these areas have been well documented (e.g., see Ungerleider and Mishkin, 1982b). The visual areas of the parietal lobe appear to have different properties from those of the ventral visual system (e.g., they include the fovea in their receptive fields less often). Second, behavioral evidence suggests that animals are severely impaired in their ability to learn to discriminate between patterns if the inferior temporal lobes are removed. However this lesion does not disrupt their ability to learn locations. On the other hand, if the parietal lobes are removed, animals are severely impaired in their ability to discriminate on the basis of location, although they retain the ability to discriminate between patterns (see Ungerleider and Miskin, 1982a,b).

This interesting design of the processing mechanisms leads to difficulties that must be overcome by the system, as is evident when we consider another problem of visual perception.

2. The Problem of Figure/Ground Segregation.

Before we can recognize an object, "figure" must be segregated from "ground"; one must somehow pick out regions that are likely to correspond to distinct objects. The magnitude of difficulty of this problem becomes evident if you look at a digitized representation of a picture, with numbers representing the intensity of light at each point; the objects are overwhelmed by differences in lighting, texture, and so on, and it is very difficult to pick them out. A figure must be selected on the basis of physical properties of the input, such as regions of homogeneous color or texture, or contiguous zero-crossings in the second derivative of the function relating intensity to position (which occur at the edges of objects; see Marr, 1982). That is,

because one has not yet identified the object (segregating its form from the background is a logical prerequisite to recognition), one can only use physical parameters to parse figure from ground. There are numerous proposals in the computer vision literature for ways of organizing input into regions likely to correspond to figures (e.g., see Ballard and Brown, 1982).

An interesting problem arises here because the visual system processes input at different spatial frequency bandwidths (see Shapley and Lennie, 1985). Higher spatial frequencies correspond to more light/dark alternations per degree of visual angle; thus, higher resolution is required to detect higher spatial frequencies. The system can be described as having a number of different "channels," each differing in resolution. At average viewing distances, the lowest spatial frequency channel produces an output that will often correspond to the general shape envelope of an object. But consider what will happen at higher spatial frequency channels: the same factors that result in the parse of the object from the background will result in parts of a single object (e.g., the arms, legs, and head of a person) being parsed from one another. That is, the system cannot "know" what is an object and what is a part of an object; it just organizes regions in the input on the basis of physical parameters of the input array. And herein lies a difficulty: Once parsed, the shape representation system "ignores" the location in the visual field of the stimulus. Thus, the representation of the shapes of the parts will not preserve their positions. But the arrangement of parts is important for many recognition tasks. The relations must be represented somehow.

The most straightforward solution to this problem requires a minor revision to the Ungerleider and Mishkin theory. It seems clear that "what" and

"where" are not so distinct conceptually: Sometimes the spatial relations among the parts are critical for identifying the form; for example, the difference between a Q with a long tail and an Q with a diagonal slash through it is a matter of where the diagonal is positioned. Rather than "where," the dorsal system seems specialized for representing spatial relations, including those among parts of a single object. The relations among high-resolution representations of parts presumably are represented the same way as are the spatial relations among separate objects in a scene. (However, note that the parts and their relations are also implicit in a low-resolution, low spatial frequency representation; for example, a handle of a mug will be a bulge on the blob-like representation of the mug.) In the relevant experiments, animals have never been required to discriminate among patterns that differ only in the relations among parts; usually stimuli differ in terms of numerous features, and the relationships among them are not important (e.g., as is true for the square and plus sign used by Ungerleider and Mishkin, 1982b, which can be discriminated between simply by looking in the center of the figure and seeing if there is a line). In short, it would appear that once figure is segregated from ground, regardless of whether "figure" is an object or part thereof, the location of that figure is represented in the parietal lobes.

3. The Problem of Non-rigid Transformations.

We can gain some insight into the way spatial relations are represented by considering another problem that must be contended with by a visual system: namely, the problem that many objects are subject to a near-infinite number of transformations, and so may not look the same from instance to instance. For example, a human form can be configured in a huge number of different ways,

crouching, arms raised, standing on one toe with the arms held out to the side, and so on. Similarly, letters of the alphabet can occur in numerous fonts, which are not simple linear transformations of each other. We cannot store a separate representation of all the possible configurations of such objects, with the aim of being able to match input to a specific stored representation—there are simply too many possible configurations, and one often may encounter configurations not previously seen. Thus, it is useful to have a representation that will be stable across a wide range of transformations. Two kinds of attributes remain constant under such transformations: First, the individual parts remain the same; although some may be hidden depending on the configuration, no parts are actually added or deleted from the object. Second, the topological relations among parts remain constant under all of these transformations. Topological relations are more abstract than the precise relative position of two parts as they appear in any given case (i.e., the topographic relations); they indicate which parts are connected to each other and which are contained within each other. For example, the topological relation between the arm and shoulder remains constant under all of the different positions the arm can take. However, literally topological relations are too weak; a teacup and a phonograph record are identical under a topological description. The relations of ears to the side of the head, or the thumb to a hand, are important and will remain constant under transformations. Thus, some general categories of relations, such as "left/right," "side of," "connected to at the end," and so on, must be used, not the actual topographic appearances.

This problem places requirements on what the dorsal system must do:

this system must be able to derive a description of relations which will remain true under a large number of ways of configuring the object. These descriptions themselves cannot be images; images are concrete, being representations of specific instances. Instead, the dorsal system must be able to make use of more abstract, "categorical" representations. Such representations capture general properties of a relationship without specifying the details (e.g., "left of" without specifying how much or exactly what angle).

Finally, it would seem necessary that at some point the representations of perceptual units and their relationships must come together. A possible locus of that nexus is the association cortex near Wernicke's area (in the posterior, superior temporal lobe), which appears to be involved in semantic processing. However, this sort of arrangement is somewhat awkward, in that the relations must be delivered in synchrony with the related units; if the inputs fall out of phase, one may make "illusory conjunctions." That is, one may conjoin units using the wrong relations. Interestingly enough, Treisman and Gelade (1980) report just such illusory conjunctions when the system is pushed to perform well in a difficult task. They found that subjects will occasionally report seeing a T when a field containing instances of | and Z was shown, which would follow if the vertical line was mistakenly conjoined with a horizontal segment from the Z.

III. PROCESSING MODULES USED IN IMAGERY

Before continuing, it will be useful to summarize where we have arrived so far. We have discussed two classes of mechanisms used in vision. The "ventral system" accesses stored representations that are associated with an

individual part or with the overall shape envelope. The representation of shape used in the ventral system should be concrete, capturing the precise shape and surface details of the part or object. This system does not process relations among parts, except insofar as they are implicit in a low resolution representation of the entire object (a kind of blurry silhouette). In contrast, we are led to assume that the "dorsal system" must be able to derive abstract "categorical" representations of the spatial relations among parts or objects. These sorts of representations group spatial relations into categories that are characterized by the presence of specific relation (e.g., "left of," "above," "next to"). The use of categorical representations of spatial relations is especially appropriate for classes of objects whose members are subject to non-rigid transformations. In these cases, the parts can be arranged in a large number of topographical configurations. For example, there is no combination of uniform linear alterations in size, orientation or position that will change an italic version of an upper case letter to a Times Roman or Geneva font and vice versa, or that will map each human postural configuration into every other. In such cases, the topological relations must be abstracted out from given exemplars. Finally, we have assumed that the information about units and relations must be combined at a later stage in processing, and that a rather tight linkage must be maintained between the dorsal and ventral systems.

Image Generation

It seems safe to assume that visual images are formed on the basis of representations that initially were encoded during perception. If so, then we are in a position to exploit the analysis presented in the previous sections to

formulate a theory of the processing modules used in imagery. The analysis of visual processing has direct implications for a theory of mental image generation. That is, images are not always in mind; when appropriate, they are formed on the basis of stored information. The question is, how are they generated?

Images must be formed on the basis of information encoded during perception. This stored information can later be compared against new input, and hence used for recognition. Thus, we can infer that images are formed on the basis of information that can also be used in perceptual recognition; the stored visual representations used in recognition are "concrete", containing enough information to allow one to reconstruct the actual appearance. The process that activates stored visual information can be conceptualized as a processing module that activates representations stored in memory to produce a pattern of activation in a "visual buffer" (this pattern of activation <u>is</u> an image representation). The purpose of this transformation is to make explicit the spatial properties of a shape, which is required to accomplish the purposes of imagery discussed earlier. The "visual buffer" is assumed to be a functionally-defined storage medium that probably corresponds to the joint operation of numerous topographically organized areas of cortex (see Van Essen and Maunsell, 1983). We assume that these visual parts of cortex also can be activated from stored information, resulting in a mental image. This buffer is equivalent to the buffer that supports Marr's (1982) "2 1/2 D sketch" in vision.

When we see patterns, we actively organize and parse them into separate perceptual units, and these units are stored (e.g., see Reed, 1974; Reed and

Johnsen, 1975). Thus, the processing module that activates stored visual information would activate representations of a previously-encoded perceptual units. Activating a stored unit could result in an image of a single part or a low-resolution image of the entire object (provided that such a unit was encoded). For convenience, let us call this module the PICTURE processing module.

If the relations among units are stored using categorical representations, then other modules must be used if a multipart or detailed object is to be imaged. We need to posit a processing module that can access the descriptions of relations and use them to juxtapose separate parts in the correct relative positions in an image. Such a module would look up and interpret a description of how parts are to be arranged. For example, in generating a detailed image of a car, it might look up "front wheel" and discover the location description "under front wheelwell." (Such a categorical representation would be used because of the great variability in the appearances of different types of cars.) For convenience, let us call this the PUT processing module.

There are two ways in which a description could specify the spatial relations among parts. On the one hand, positions could be specified in terms of absolute location. On the other hand, positions could be specified relative to other parts. If objects are subject to non-rigid transformations, the absolute location of parts will change depending on the configuration. Thus, for the same reasons we hypothesize that categorical representations are used for spatial relations during recognition, we also posit that these representations specify relative locations: such representations will remain

constant under various transformations. For example, an arm is connected to a shoulder regardless of how the person is postured.

Thus, if relative positions are used, then one must know the location of a reference point in order to add a part to a multipart image (e.g., the "wheelwell," for a car's wheel, or the shoulder for an arm); only after locating the reference point will one be able to position another part correctly in an image. In order to locate a reference point, a third module must be used. This module needs to search for a specific part, which is one function that requires the ventral visual system. For convenience, we will call this module the FIND processing module. The PUT processing module uses the output from the FIND processing module (e.g., the location on the wheelwell on the car's body, where the front wheel belongs) plus the description of the relation ("under") to compute parameter values for the PICTURE processing module, allowing it to form an image of the new part in the correct relation to the foundation part.

Image Transformations

Our analysis of visual image transformations begins with the observation that for some tasks we need more than a categorical relation among parts. For example, in navigating in the dark you need to know exactly where various pieces of furniture are located in the room, not simply their relative positions. Similarly, in recognizing faces you need to know the metric spatial relations among features, not simply their general positions. Thus, we apparently need <u>two</u> ways of representing positions: categorical relations and coordinate positions within a specific frame of reference (e.g., a room or face). Image transformations, such as moving the position of an object in an

imaged scene, or altering its orientation, involve changes in metric spatial relations. Thus, they presumably require altering the coordinate representations of locations.

The most basic finding about image transformations is that the transformation process typically is incremental; the process alters the representation of position so that the transformed object moves through a trajectory, occupying intermediate positions as it is being transformed (see Shepard and Cooper, 1982). The evidence for this assertion rests on chronometric data, such as the finding that more time is required to rotate or exapand an imaged object progressively greater amounts (see Figure 2). We can account for this property of image transformations with the following assumptions: 1) High-resolution images of objects are composed by activating stored encodings of distinct parts. This assumption follows from our analysis of image generation. 2) The representations of the locations of parts are manipulated individually when the image is transformed. This idea follows because a coordinate representation must be manipulated when one needs to alter a viewer-centered repesentation, such as by changing orientation or size; categorical representations do not embody the metric spatial relations among objects or parts (indeed, such representations are used to abstract out what is constant over such variations). In the coordinate representation, the location of each separate part is specified as a separate representation. 3) The behavior of the brain is subject to random perturbation. This observation is true of all physical systems; "noise" is pervasive. 4) Therefore, the locations of parts of an imaged object are not altered equally with each increment of transformation; there is noise in the movement operation, and the

parts become misaligned. 5) In order to realign the locations, there must be a representation of spatial relations that does not change with different coordinate positions of the parts. I have argued earlier that just this type of "categorical" relation is encoded during perception, and is used to generate images of non-rigid objects.

Presumably, the amount of misalignment is proportional to the size of the shift (i.e., variability is usually proportional to the mean), with larger shifts resulting in greater scrambling. This notion would explain why images are transformed in a series of small increments: if the positions are too scrambled, it will be difficult simply to identify the corresponding parts and to use stored descriptions to realign them.

This analysis leads us to posit two additional processing modules: One module is required to alter the representation of the positions of parts of an imaged object. We presume that this operation involves updating coordinate representations in the dorsal system. We can call this the MOVE processing module. A second module is required to look up and use descriptions of the spatial relations to direct the MOVE module to realign any misaligned parts. We can call this the CLEANUP processing module. Finally, the FIND module must also be used in image transformations. The CLEANUP module must make use of the FIND module to discover the current locations of the parts, which is necessary before it can compute how to realign them; this use of the FIND module is analogous to its use by the PUT module during image generation. (In addition, in some tasks the FIND module presumably is used to locate the top of the object to provide information about the shortest way to rotate; it presumably also is used to make the requisite judgment when the object has been

transformed far enough.)

One way we sought evidence for our analyses of high-level visual processing was by looking for "functional dissociations" among the modules we have posited. That is, we wanted to show that the two cerebral hemispheres had different abilities, which corresponded to having different sets of processing modules. In order to see how the predictions were made, however, we must understand the bases for our expecting different modules to be localized differently in the brain. Thus, we now must turn to that aspect of the theory.

IV. MECHANISMS OF HEMISPHERIC DIFFERENTIATION

The theory as stated so far, then, posits a set of processing modules and some types of representations on which they operate. The approach we have taken suggests that the functional organization of the system is a consequence in part of the kinds of information-processing problems that must be solved (c.f., Marr, 1982). The best solutions to the problems presumably influence functional organization in two ways: First, the brain presumably evolved to solve those problems efficiently, and hence the evolution of brain structure may have been shaped by the computational problems. Second, the experience of the individual organism in dealing with the problems may engender the development of a specific functional organization. The present theory is concerned with the mechanisms that result in an individual's experiences shaping the functional organization of the two hemispheres of the brain. This theory rests on a set of relatively simple, uncontroversial properties of the brain; what is original here is putting them together and observing the consequences as they interact. The relevant properties are as follows:

1. Processing components. The brain is functionally organized into a

collection of separate processing modules. This claim is supported by the subtle and distinct patterns of fractionation that are evident in the behavioral dysfunction following brain damage (e.g., see Heilman and Valenstein, 1979). Presumably, the behavioral deficits reflect damage either to some of the modules proper and/or to their interconnections (c.f., Geschwind, 1965). This arrangement makes sense if the system evolved piecemeal, with new components being added, or old ones being modified, to work with those already available. A modularized system is easiest to alter, as computer programmers have long-since discovered.

2. Exercise. A "processing module" is a functional description of what is done by a neural network. If such a network is subjected to the same pattern of input repeatedly, the subsequent internal pattern of activation and subsequent output will come to be achieved more quickly and/or more reliably. Such "practice effects" presumably reflect actual physical changes at the cellular level. We need to posit something like this principle to explain the very basic finding that practice improves the performance of even the simplest tasks. This idea goes back at least as far as Hebb (1949). In short, a processing module becomes increasingly efficient at carrying out a specific computation as it is used to do so increasing numbers of times.

3. Selectivity. A processing module can only operate on one input at a time. This claim is almost definitional, given that a given neuron can only be in one state at any given moment in time. Hence, a set of neurons can only be in one state at a time, including those neurons that serve as input to a neural net. We can regard the input to a module as a vector (values on the input lines to various neurons). If so, then a given module will receive only one

vector as input at any given moment; it is physically impossible to have two vectors being processed simultaneously, given that this would require that at least one input neuron be in two states simultaneously. And if two vectors were intermixed, it would be impossible to sort out which values go with which input vector and the input would be uninterpretable.

4. "Central" bilateral control. Some activities involve executing rapid sequences of precise, ordered operations that extend over both halves of the body. In such cases, one does not want to have the operations carried out by both hemispheres; given the physical separation of the hemispheres, it would be difficult to keep the processes synchronized. This idea implies that a relatively rapid ordered sequence of precise operations that extend over both halves of the body will be controlled in a single locus. For example, when one is speaking rapidly, one does not want to have to control the left and right sides of the speaking apparatus separately, synchronizing two sets of commands. Thus, the area that controls speech output is on only one side of the brain (typically the left) and is situated near the motor strip (precentral gyrus). Similarly, in programming rapid shifts of attention over an object or scene, one does not want to have to coordinate corresponding operations in the two sides of the brain. Thus, in most right-handed males the right parietal region appears to have a special role in directing attention (for a review see chapter 4 of De Renzi, 1982).

I had originally thought that these four properties of the brain operating together would be sufficient to produce functional differentiation between the two hemispheres. The theory was as follows: First, I assumed that differentiation develops over age and experience, as a child has occasion to

develop and use language and to learn his or her way about in the environment. The mechanism underlying this sort of differentiation depends critically on the property of "bilateral control". This property leads us to expect innately-determined assymetries in modules that utilize rapid, precisely ordered bilateral sequences of operations. (I do not have a theory as to why some of these modules are predominantly stronger on the left side whereas other modules are predominantly stronger on the right side.) These innately lateralized modules putatively come to serve as the initial "seeds" (in a catalytic sense) in the differentiation process. For example, consider first differentiation in "categorical" representation and use: An initial "seed" module, which is innately stronger on the left side, is a "speech output area". This area coordinates the mouth, tongue, and vocal apparatus to produce phonemes. Given this beginning asymmetry, I thought that the other three principles would produce a snowball effect: Initially, there are modules in both hemispheres that produce output used in making speech sounds (e.g., that set up programs to order sounds). These modules apparently are located in what is called Broca's area on the left side. The modules on the left side are relatively close to the speech output area, and hence will be selected over the corresponding modules in the right hemisphere. That is, the additional time necessary for the trip over the corpus callosum from the right hemisphere will result in the left-hemisphere processing modules being selected more often than the corresponding ones in the right hemisphere. This sequence of events will, via the property of exercise, result in speech-related, and then language-related, modules becoming stronger in the left hemisphere. Once these modules are stronger on the left side, the effect then compounds: now these

modules play the same role as did the speech output area in the differentiation process. Modules that make use of these previously-differentiated modules should themselves become strengthened in the left hemisphere. The result of this snowball effect should be that modules that make use of categorical representations, which can be manipulated by rule systems (such as those used in language and arithmetic), will in general become stronger in the left hemisphere. This notion is supported by evidence from studies of stroke patients and split-brain patients that the left-hemisphere has a special role in arithmetic and inference (see Heilman and Valenstein, 1979).

The theory as stated so far turned out to be inadequate when we got to the stage of actually building a computer simulation model. Two deficiences became apparent almost immediately: First, given that the modules that send information to the "seed" module (which is lateralized on one side) have produced an output, they have been exercised; they do not "know" whether or not their output was used. Thus, both the corresponding left and right modules are strengthened; the system will not lateralize as planned. Second, what is stopping the output from one module from interrupting the output from another? That is, although the property of selectivity ensures that the output from only one module will serve as input to another at any given time, there was no reason why a late-coming input could not supplant a previous one. The problem here is that if enough competing inputs are present, the target module may never receive consistent input long enough to be able to use it. A neural network will not produce a consistent output unless the input is maintained over a period of time. That is, it takes time for a network to settle into a stable pattern of activity, and the same input must be maintained during the

course of this settling down process (e.g., see Ackley, Hinton and Sejnowski, 1985). (Technically, the input lines must be "clamped" long enough for the network to settle into equilibrium.) If the network is not at equilibrium, it will not systematically produce a single output when given an input.

Fortunately, a fifth property of the brain, previously not considered relevant, seems to solve both problems for us:

5. Reciprocal innervation. A fundamental fact about the visual system is that most of the pathways have both afferent and efferent tracks (Van Essen and Maunsell, 1983). This property of the system could be used as a way of maintaining an input long enough for a network to make use of it. In order to maintain an input, the efferent pathways could be used as a feedback loop, stimulating the source of the input. That is, the brain is not a digital computer; it does not pass discrete symbols back and forth. Rather, we assume that modules produce patterns of activity, which can be sustained if the module is driven to do so. While the output from one sending module is being sustained, the target module cannot receive the output from another module; the sending and target modules are "locked" into a loop. Thus, the property of selectivity can be regarded as a consequence of the property of reciprocal innervation, and need not be treated as a separate property of the mechanism.

A snowball theory of differentiation

Thus, the mechanism of differentiation just described becomes modified: once an input arrives at a module and is entered into it, the output from the sending module will be sustained. If so, then only the module that produces output that arrives to the target module first will be stimulated, and hence exercised. Furthermore, the feedback loop can serve to "lock in" an input

until the network has settled, which solves the problem of multiple interruptions. Thus, the theory rests on the ideas that a) "seed" modules are initially lateralized; b) when the output from a module serves as input to a seed, feedback from the seed module drives that sending module until the seed has settled (i.e., interpreted the input); c) during this period, the sending module is exercised, resulting in its becoming faster and more noise resistant when used in the same way in the future. Only the module whose output is actually used becomes exercised; the output from the corresponding one on the other side is not used (is selected against), and hence it is not driven to remain in the output state long enough to become exercised. This process is repeated with "second-order seeds", modules which themselves are not innately lateralized but that become so during the course of experience.

This mechanism, then, will result in the left hemisphere's becoming specialized for using categorical representations. These representations are well-suited for specifying pairwise relations among parts (e.g., a hand is connected to a wrist, a wrist to a forearm, etc.). They are not well-suited, however, for representing graded, topographic information nor for representing locations in absolute space. In most people, the right hemisphere appears to have become relatively specialized for these functions (see De Renzi, 1982). The theory for this development is analogous to the theory of development of categorical representation, only in this case the property of central bilateral control underlies a unilateral locus for one component of our attentional mechanism, namely that involved in directing shifts in attention. (We must be careful here, however; at present there are at least four loci implicated in attentional shifts—the right parietal, frontal eye fields, superior

colliculus, and reticular activating system; see Mesulam, 1981.)

The present claim, then, is that the parietal lobe represents spatial relations, and can do so in two ways: in terms of a given category of spatial relation or in terms of coordinate points in space. Because metric information is necessary for planning attentional shifts, the modules that produce the metric map become exercised and stronger in the right hemisphere. Thus, the proposed mechanism will result in the right parietal lobe coming to represent spatial relations by using coordinate points in a metric, analog "map" of where objects fall in the space around an organism; in contrast, the left parietal lobe will come to represent relations categorically. This conjecture allows us to explain much data on the right hemisphere's superior topographic ability (see Byrne, 1982) and ability to represent metric location (e.g., see Kimura, 1969). The topographic information in the right hemisphere is especially critical for purposes of navigation: Simply knowing that one object is not connected to another does nor tell you if there is enough room between them to put your foot. Thus, modules concerned with representing space for use in navigation also will come to be stronger in the right hemisphere.

The theory as developed so far posits that the ventral visual system is not lateralized; it is simply duplicated on both sides of the brain. This duplication occurs because the output is used directly in both hemispheres, and so both sets of modules are exercised. In the left hemisphere, however, the output is converted to categorical representations (perhaps using "symbols," with conversion occuring via the polysensory association areas and then Wernicke's area); in the left hemisphere the relations among parts, putatively processed in the dorsal visual system, are represented in a categorical format.

In the right hemisphere, in contrast, the output from the ventral system is not converted into a categorical form. Rather, usually there may not be an analog to Wernicke's area, which converts input to a semantic form. (A rare individual may violate this generalization, however; see De Renzi, 1982.) Furthermore, the relations represented in the right hemisphere dorsal system will not be categorical. Rather, objects' locations are specified in a topographic map of space, and the relations are relative to a single reference point (the origin of the coordinate space); inter-part relations are only indirectly specified. The possibility of representing spatial relations in two ways suggests that the hemispheres will have different roles in performing spatial tasks.

Lateralization of Imagery Processing Modules

The theory of hemispheric differentiation leads us to expect that the PUT processing module will be more efficient in the left hemisphere. This prediction follows because this module must access and interpret categorical representations. Presumably, the intepretation of these representations makes use of other modules that are also recruited in language processing. If so, then the snowball theory described above will result in the PUT module becoming more effective on the same side as these modules. In contrast, the PICTURE module should be equally effective in both hemispheres. The visual representations on which it operates are duplicated in both temporal lobes (see Gazzaniga, 1970). Thus, there is no reason to think that the activation of these stored representations should be favored on one side over the other. Similarly, the FIND processing module should be equally effective in both hemispheres. The visual buffer is duplicated in both hemispheres (each

representing the contralateral hemifield), and the FIND module should be used equally often in processing each side.

The theory also allows us to make predictions about the ease of mental rotation in the two hemispheres. We expect the two hemispheres to be involved in different ways in mental rotation. As was discussed earlier, the rotation of complex figures should require use of descriptions to realign the parts as they become scrambled during the rotation process. The CLEANUP (realign) module will become more effective in the left hemisphere for the same reasons that the PUT module should become more effective in the left hemisphere. In contrast, the repositioning operation performed by the MOVE module depends on altering the topographic representation of the layout of individual parts. The modules that produce this representation are more effective in the right hemisphere. The theory thus predicts that the MOVE module will become more effective in the right hemisphere.

IV. NEUROPSYCHOLOGICAL EVIDENCE FOR LATERALIZATION OF THE IMAGE GENERATION MODULES

If our theory of the functional organization of high-level vision is correct, we should be able to find a sort of brain damage that leaves some of the modules intact while disrupting the others. Furthermore, if the theory of lateralization is correct, we should be able to discover selective deficits in the two hemispheres. Thus, we began by investigating a counterintuitive prediction, namely that the left hemisphere should be better than the right at selected imagery tasks. This prediction rests on there being a dissociation between the three modules purportedly used to generate visual mental images (for details see Kosslyn, Holtzman, Farah, and Gazzaniga, in press). We sought

a dissociation between the FIND and PICTURE modules on the one hand, and the PUT processing module on the other. The idea was that the PUT processing module involves manipulation and use of categorical representations of the type used in linguistic processing, and hence our "snowball theory" led us to expect that such processing would typically be localized in the left hemisphere (the locus of linguistic abilities, at least for most right handed males). In contrast, the theory leads us to expect the FIND and PICTURE modules to be equally effective in both hemispheres (as was discussed in the previous section). Thus, we hoped to show that the left hemisphere could perform image generation tasks that involved all three modules, whereas the right hemisphere could perform tasks that required only the PICTURE and FIND modules. This prediction was especially interesting because the common wisdom has it that the right cerebral hemisphere is the seat of mental imagery (e.g., see Springer & Deutch, 1981; Ley, 1979; Ehrlichman & Barrett, 1983). Thus, if we can show that the left hemisphere is actually able to perform a wider range of imagery tasks, this will be particularly dramatic evidence of the usefulness of the computational approach.

Imagery validation. We first showed that imagery was required to perform a task that putatively recruited all three image generation modules. The task was to decide from memory whether upper case letters of the alphabet were composed of all straight lines (e.g., K, L) or had some curved lines (e.g., B, R). Our demonstration used the selective interference logic developed by Brooks (1967), Segal (1971), and others. These researchers showed that imaging and perceiving in the same modality interfere with each other more than do imaging in one modality (e.g., visualizing a flower) and perceiving in

another (e.g., listening for a tone). We used a technique developed by Brooks: He asked subjects to visualize block letters and then to classify the corners (working clockwise around the letter) according to whether they were on the extreme top or bottom of the letter. For each corner, subjects were to respond by either saying "yes" or "no" aloud (as appropriate) or by pointing to "y" or "n" on a page, working down crooked columns of the letters over the course of the task. Having to look for and point to the letters was much more difficult in this task than merely saying "yes" or "no". In contrast, in another task subjects formed auditory images of spoken sentences and decided if each word was a noun or not. Now saying the responses was harder than pointing to them. The idea was that visual perception interfered more with visualizing, but talking (and hearing) interfered more with auditory imaging.

We made use of Brooks' task to garner evidence that the straight/curved letter judgment requires imagery. College students read down a column of lower case letters, and made the straight/curved judgment about the corresponding upper case versions. These subjects were asked to respond either by putting a check mark in the appropriate location on the page (which required looking for the place to respond) or by saying the response aloud. Looking and making check marks required more time, even though making check marks in isolation actually took less time than saying the response. These results in conjunction with the earlier findings implicated imagery in this task (see Kosslyn, Holtzman, Farah and Gazzaniga, 1984).

The next task was to demonstrate that images of upper case letters are generated a segment at a time. This was important because the theory says that the PUT processing module is only used when separate parts must be amalgamated

into a composite image. We reasoned that people have seen so many upper case letters that they do not image a particular one actually seen when asked to image a letter. When the reader imagines an upper case "a", it probably is not one actually seen at some point in the past; rather, a "prototypical" A is probably imaged. We assume that the characteristic features of A's have been abstracted out and stored as a description, something like "two slanted lines of roughly equal length meeting at the top, joined roughly halfway down by a horizontal line". (Although English is used to write the description here, some other code may be used in the brain; perhaps the descriptions are stored more like instructions in a computer.) To test the claim that images of letters are created a segment at a time, Kosslyn, Backer and Provost (submitted) showed subjects two x marks in an otherwise empty 4 x 5 grid and asked them whether both x's would fall on a given upper case letter if it were present in the grid (as the letter appeared when it was actually presented previously). If the segments are imaged individually, then some will be present before others. If so, then the time to affirm that the x marks would fall on the letter will depend on the location of the segments on which they fell. And indeed, the location of the x marks proved to be critical in the imagery condition, with more time being required for marks that fell on segments located towards the end of the letter (i.e., towards the end of the sequence of drawing it). A number of controls were used to ensure that image generation, and not image inspection after the letter was formed, was responsible for the effects.

The upshot of the preliminary work, then, was that images of upper case letters are usually generated a part at a time—which requires descriptive

relations among the parts, according to our theory—and that imagery is used to decide if named upper case letters have any curved lines. The weak link here, of course, is the assumption that because letters are imaged a part at a time they must be imaged on the basis of a stored description. There is a computational argument in support of this assumption, based on the large variability among instances of letters (as noted above), but it is enough simply to point out that if the experiments had not come out as predicted it may have been because this assumption was faulty.

An Imagery Deficit

Thus, we began by investigating whether both hemispheres of patient J.W. could perform the straight/curved imagery task. J.W. had his corpus callosum sectioned about 3 years prior to our testing because of severe intractable epilepsy; he has been extensively tested and his right hemisphere is capable of comprehending involved verbal instructions and of making simple deductions and classifications (see Sidtis et al., 1981, for further details).

In order to isolate performance to a single cerebral hemisphere, we asked J.W. to stare straight ahead at an asterisk on a screen and flashed lower case letters to the left or the right side of this fixation point. As is illustrated in Figure 6, the construction of the retina and optic nerve ensures that a lateralized stimulus is exposed to only one hemisphere, given that the corpus callosum is severed and hence interhemispheric communication is precluded. We asked J.W. to look at the lower case letter and to decide if the upper case version had any curved lines. He pressed one button if he thought the upper case letter had curves, and another if he thought it had only straight lines. The left arm was used for all responding (due to ipsilateral

efferents, both hemispheres can control the major arm movements; fine motor movements are controlled only by the contralateral hemisphere).

INSERT FIGURE 6 ABOUT HERE

The task, then, requires use of seven abilities (each of which is presumably carried out by a host of processing modules): First, the lower case letter must be ENCODED. Second, it must ACCESS the representation of the upper case version. Third, the image of the upper case version must be GENERATED. Fourth, the image must be RETAINED long enough to be judged. Fifth, the image must be INSPECTED. Sixth, a JUDGMENT must be made. Finally, a RESPONSE must be produced. Our first goal was to demonstrate that the right hemisphere had a deficit in performing the task, and then to show that it was due to a problem in GENERATION per se. Following this, we sought to implicate a specific dissociation between the PUT processing module and the other two processing modules.

The results from the first sets of trials were straightforward: J.W.'s left hemisphere made straight/curved judgments virtually perfectly, but his right hemisphere was almost at chance performance. A number of control experiments were conducted to implicate a deficit in image generation per se. First, we lateralized upper case letters and asked J.W. to perform the judgment on the actual stimuli. Both hemispheres were virtually perfect. Thus, both hemispheres could ENCODE the letters, INSPECT them, make the JUDGMENT, and produce correct RESPONSES. In another control, we lateralized the lower case versions, and simply asked J.W. to select the corresponding upper case version

from the alphabet, which was displayed in free view. Both hemispheres were virtually perfect; thus the right could ACCESS the cross-case representation. Indeed, both hemispheres could even draw the upper case letters (using contralateral hands) after seeing the lower case cue, even when the hand was obscured from view (drawing under a table).

In another control, we lateralized 3-letter words; the words were composed of upper case letters (e.g., MUG). J.W. was then cued two seconds later as to which letter (first, second, or third) to classify as being straight or curved. Both hemispheres could do this task; in fact, the hemispheres performed as well as when the cue was given beforehand, and no imagery was required. Thus, the problem was not that the right hemisphere could not RETAIN the image long enough to inspect it, nor was the problem that it could not INSPECT images.

At this point we had demonstrated that the right hemisphere could perform all of the sub-tasks except image GENERATION. However, other possible accounts needed to be eliminated. Perhaps the right hemisphere could not combine sub-tasks. Thus, in another control, we showed pairs of letters, one upper case and one lower case (both drawn at the same size); on half the trials the upper case was on the left side, and on half it was on the right side. The slides were lateralized, so that only one hemisphere saw the pair. We asked him to point to the upper case version and to classify it. His right hemisphere clearly knew the differences between cases, and could do a two-step task. The word-retention task described in the previous paragraph also required integrating multiple steps (ENCODING the stimulus, RETAINING and image, SELECTING the correct letter, INSPECTING the image, JUDGING the shape,

and RESPONDING).

To investigate possible "Stroop" sorts of interference, where the lower case stimulus somehow interfered with the upper case task, we read him letters aloud (and thus both hemispheres knew which letter was being queried). Now the pair "X O" or the pair "O X" was presented to a single hemisphere. The task now was to point to the place on the screen where the X had been if the upper case letter had only straight lines and to the location where the O had been if the upper case letter had any curves. Again, the left hemisphere was virtually perfect, whereas the right hemisphere was at chance. Thus, the right hemisphere's poor performance was not due to a conflict between the visible lower case version and the imaged upper case version.

Both hemispheres could perform the judgment on visible stimuli, could perform it when the image was simply retained from external input, could make the association between upper and lower case, and could perform tasks of similar complexity involving selecting a case and making the judgment. And the right hemisphere's difficulty in performing the imagery task did not appear to be in understanding the instructions; the other multistage tasks had comparably difficult instructions, and J.W.'s right hemisphere has been shown to understand complex instructions in other tasks (see Sidtis et al, 1981). Nor did its problem lie in combining subtasks, or in having interference from the lower case stimuli themselves. It appeared that J.W.'s right hemisphere simply could not generate images of the letters.

A Selective Imagery Deficit

The results described so far serve only to demonstrate an image generation deficit in J.W.'s right hemisphere. They do not implicate a deficit

in one processing module or another. In order to implicate a deficit in using the PUT processing module per se, we needed to show that both hemispheres could use the PICTURE and FIND processing modules. These are the only processes required to generate images of the general shape of an object, if such a shape was encoded as a single low-spatial frequency perceptual unit. And in fact, we discovered that both of J.W.'s hemispheres could perform tasks requiring the imaging of overall, general shapes: In one, we asked each of J.W.'s hemispheres to decide which of two similar-sized objects (e.g., goat vs. hog) was the larger, a task previously shown to require imagery (see chapter 9, Kosslyn, 1980). J.W. stared at a central fixation point, and a word was presented to one side or the other. If a goat was larger than the animal named by the word, he pushed one button; if the word named an animal larger than a goat, he pushed the other button. Both hemispheres performed this task virtually perfectly, with no difference in either the error rates or response times. He also could decide equally well in both hemispheres whether a named object was higher than it is wide. These tasks require the PICTURE processing module to generate images of the general shapes of the objects, and the FIND processing module to inspect the objects in the image. Because no parts need to be added to the general shape to perform either task, the PUT module is not necessary. (Incidentally, these results are also important because they show that the right hemisphere's problem is not simply in processing letters, which are linguistic materials.)

We also conducted another task that should require the PUT module. This task made use of exactly the same materials used in the size-judgment task, which both hemispheres could perform equally well. Now J.W. was asked to

decide if the named animals did or did not have ears that protrude above the top of the skull (e.g., an ape and a sheep do not, a cat and a mouse do). One response button was labeled with an inverted U (representing the top of the animal's head) with a triangle sticking above it; the other had the inverted U with a small u hanging down. The names of the animals were presented to the individual hemispheres, and they categorized their ears (J.W. lived on a farm and is quite familiar with animals). The left hemisphere made very few errors, whereas the right hemisphere performed at chance.

These results, then, showed that J.W.'s right hemisphere could perform imagery tasks that require use only of the PICTURE and FIND modules, but could not perform tasks that also require use of the PUT module.

V. NEUROPSYCHOLOGICAL EVIDENCE FOR THE TRANSFORMATION MODULES

The theory leads us to expect that the right hemisphere will be better at actually transforming the representation of relative location. There is some suggestive evidence that this may be true. For example, Ratcliff (1979) found that subjects with right parietal lobe damage have difficulty performing a simple mental rotation task. Similarly, Weisenberg and McBride (1935) found that such patients have difficulty in deciding whether two shaded sides of an unfolded cube would be adjacent when the sides were folded to form the cube, and Le Doux, Wilson, and Gazzaniga (1977) found that the isolated right hemisphere of a split-brain patient was better at spatio-manipulation tasks. However, other studies have provided mixed evidence for a simple right-hemisphere specialization for image transformations (e.g., see Butters, Barton, and Brody, 1970; De Renzi and Faglioni, 1967; see chapter 6 of De Renzi, 1982 for a review). Similarly, studies of normal subjects receiving

lateralized stimuli have produced mixed results (see Cohen, 1982; Simion, Bagnara, Bisiacchi, Roncato, and Umilta, 1980). Overall, the findings can most easily be interpreted as indicating bilateral involvement, which is not surprising if the present theory is correct.

The theory also leads us to expect that a left-hemisphere module will be used when complex shapes are transformed in an image. Kosslyn, Berndt, and Doyle (in press) report results that support this claim. Two aphasic patients were tested, both of whom had severe left-hemisphere damage; one patient corresponded quite closely to the classic syndrome of Broca's aphasia and one corresponded quite closely to the syndrome of Wernicke's aphasia. These patients were asked to image two-dimensional analogues of the Shepard-Metzler stimuli illustrated in Figure 1. These shapes were formed by selecting five cells in a 4 x 5 grid that were each connected to at least one other cell, and eliminating all but these cells (producing a set of connected boxes). The subjects were shown a pair of these forms, and asked whether they were identical irrespective of orientation about the circle; the left form was always vertical and the right was at a variety of orientations. On half of the trials the two forms were identical, and on half they were mirror-reversals of one another. The results were clearcut: both patients showed decrements for mental rotation. Indeed, the rate of rotation was almost an order of magnitude slower than that of a control group. This finding suggests that the left hemisphere plays some role in the rotation of complex forms.

The critical test of the theory of image transformation will be to compare performance on multipart stimuli versus single part stimuli (e.g., of the sort used by Marmor and Zaback, 1976). If the theory is correct, the

CLEANUP module is required only with multipart stimuli. If so, then the putative right-hemisphere superiority with the MOVE module ought to be apparent when one-part stimuli are used.

VI. NEUROPSYCHOLOGICAL EVIDENCE FOR SPECIALIZED REPRESENTATIONS OF RELATIONS

A major claim of the theory is that the "dorsal" system becomes differentiated in the two hemispheres. The left dorsal system putatively becomes more effective at assigning a spatial relation to a category, such as "left of" or "attached to". The right dorsal system putatively becomes more effective at representing position as a point in space relative to a single origin. Kosslyn and Barrett (in preparation) set out to test this claim directly in two simple experiments: First, subjects (normal college students) were shown stimuli like those illustrated in Figure 7. These stimuli were line drawings of blobs, with a dot being either on the line or outside of it. The subjects were asked to fixate directly ahead, and a stimulus was presented to one side or the other. For one set of trials, the subjects were to respond "true" if the dot was on the line, and "false" if it was off the line. For another set of trials, the subjects were to respond "true" if the dot was within 2 mm of the line, and "false" if it was farther than 2 mm from it (subjects were shown what a 2 mm distance looked like at the beginning of the experiment). Our prediction was that the left hemisphere would be more effective at categorizing the dot/line relation as "on" or "off," whereas the right hemisphere would be more effective at representing the metric spatial relation. As is evident in Figure 8, these predictions were borne out: The on/off judgment was easier when the stimuli were presented to the left

hemisphere, whereas the near/far judgment was easier when the stimuli were presented to the right hemisphere. The near/far task was also easier in general, which reflects the particular stimuli we used (the distances were such that the discrimination was relatively easy).

A second experiment was conducted to provide convergent evidence for the claim. Now, subjects saw stimuli consisting of a plus and a minus sign, placed side by side. On half the trials the plus was on the right, and on half the trials the plus was on the left; in addition, on half of each of these types of trials the stimuli were less than 1 inch apart, whereas on the other half they were greater than 1 inch apart. Subjects again began each trial by fixating straight ahead, and a pair of stimuli was lateralized. Subjects again participated in two sets of trials. In one, they simply decided whether or not the plus was to the right of the minus. We expected the left hemisphere to be better at this sort of categorical judgment. In the other set of trials, the subjects decided whether the stimuli were closer or farther than an inch apart. We expected the right hemisphere to be better at this sort of metric judgment. These expectations were confirmed, as is illustrated in Figure 9.

INSERT FIGURES 7, 8, 9 ABOUT HERE

The present theory is also consistent with numerous findings already in the literature. For one, it is typically reported that different types of deficits in drawing occur after damage to the left or right hemisphere (see De Renzi, 1982). When the right hemisphere is damaged, the drawings often contain correct details, which are locally organized correctly, but the global

organization is awry. The effects of right hemisphere damage would be to disrupt the coordinate, single-origin, representation. Thus, the overall coherence of form will be disrupted; when the left hemisphere is operating alone, it will have the local pairwise relations, but not the overall form. In contrast, when the left hemisphere is damaged, the drawings preserve the global organization but lack detail. Presumably, without the PUT module, parts of nonrigid objects will not be able to be placed in their correct relative locations. For rigid objects (i.e., those which have a single version in which parts are rigidly arranged), on the other hand, we have no reason to expect a right hemisphere deficit.

The present theory, then, predicts that the hemispheres should deal with rigid and nonrigid objects in different ways. A face of an individual person is an example of an object that is essentially rigid. That is, the location of the eyes, eyebrows, nose, ears, hairline, and mouth do not vary. Facial expressions change the shape of parts, but do not alter their positions. In addition, the metric relations among the parts is not something to be ignored in recognition, as is the case with the various configurations of the parts of nonrigid objects (e.g., the configuration of the limbs of a person). Thus, it is interesting that the right hemisphere seems to have a special role in face recognition. It is well-documented that the right hemisphere is better able to recognize faces than the left (e.g., see Gazzaniga and Smylie, 1983). In most cases, the relations among parts must be preserved if a face is to be recognized, so these data are prima facie evidence that the right hemisphere is in fact preserving the relations among parts of faces (although I claim that the relations are relative to a single origin, not pairwise). Note, however,

that some faces can be recognized on the basis of distinctive characteristics (e.g., Nixon's jowls and nose), and so the left hemisphere should be able to recognize faces using this sort of information (see Diamond and Carey, 1977; Etcoff, in press). To my knowledge, no one has systematically investigated how left-hemisphere damaged patients draw faces. This would be difficult to do because left hemisphere patients will often suffer from aphasia (making it difficult to convey the instructions) and right-side hemiplegia (making it difficult, or impossible, to use the right hand). In addition, drawing is a problematic dependent measure even with right-hemisphere damaged patints, given that the damage can cause disruption to output modules in the right hemisphere, which would mask the intact functioning of the representational system feeding into these modules.

In the same vein, we can also account for the findings of Martin (1979) and Sergent (1982) on preferred level of analysis of the two hemispheres. This research was derived from that of Navon (1977), who showed subjects large letters that were constructed by arranging numerous copies of a small letter. Subjects were asked to look for target letters, which could be presented either as a large, composite figure, or as smaller, constituent figures. Navon found a "global precedence" effect, with subjects detecting large targets faster than small ones. It is interesting that when stimuli of this type were lateralized in the experiments of Martin (1979) and Sergent (1982), the left hemisphere was faster when the target was the small letter, whereas the right hemisphere was faster when the target was the large letter.

Our account of these results again rests on our analysis of the purposes of the left and right hemisphere spatial representational systems. I

have argued that the coordinate representation in the right hemisphere is used primarily in the service of navigation. If so, then information about small spatial variations (details) may be used less often than information about more coarse variations. In this case, the modules that process coarser information will come to generate coordinate representations more quickly (because of the principle of exercise) in the right hemisphere. These representations may then be template-matched against representations of rigid-patterns stored in the right hemisphere. This operation presumably can be performed very quickly, more quickly than generating descriptions of the interpart relations and comparing them to stored information in the left hemisphere. On the other hand, the left hemisphere system purportedly categorizes parts and relations among them. Hence, the modules that represent information about parts presumably come to be more effective in the left hemisphere.

The present account of the hemispheric specialization results is supported by the finding that the "global precedence" effect (found when stimuli are not lateralized) can be eliminated if the large pattern is distorted (Hoffman, 1980). If the present theory is correct, this manipulation would impair the matching against rigid patterns stored in the right hemisphere. When the input pattern is distorted, it can no longer be easily matched against such a rigid template, and the left-hemisphere system becomes relatively more effective.

VII. CONCLUSIONS

This paper has attempted to illustrate the value of using a computational approach in conjunction with neurological data and methodologies from cognitive psychology. The results of taking seriously the neurophysiology

and neuroanatomy have been somewhat surprising. On the face of things, the notion of splitting apart processing of parts from processing of relations seems counterintuitive to many. In addition, it was something of a surprise to discover that imagery should be selectively better for some tasks in the left hemisphere. The standard view that imagery is a right hemisphere function is incorrect.

But is the present approach really an advance over a more common sense, intuitive approach? Yes, it is, for two reasons: First, the usual accounts are always vague. For example, what does it mean to say that the right hemisphere is "perceptual"? Many researchers in artificial intelligence (e.g., see Winston, 1975) claim that perceptual representations are not different in kind from language representations. Or what does it mean to say that the right hemisphere is "intuitive"? Or "synthetic"? and so on. The computational approach introduces precision, which allows theories to generate clear predictions. Second, the present approach is an advance over a more common sense, intuitive approach because those theories are often incorrect. To the extent that they make concrete claims, they are usually overly general and coarse. To cite the present example, imagery is not a left or a right hemisphere function. "Imagery" is too coarse a level of analysis; the function decomposes into numerous sub-abilities, which in turn are carried out by numerous processing modules. To further complicate matters, some of these modules may be dedicated to a particular ability (e.g., the MOVE module), whereas other modules may be used in carrying out a number of abilities (e.g, the FIND module, which purportedly is recruited in image inspection, generation, and transformation). And the individual processing modules need

not be lateralized in the same way. The computational approach is ideally suited for decomposing abilities into components, which gives one enormous conceptual power in analyzing the functional differences between the hemispheres.

Perhaps the greatest promise of the present approach over previous ones lies in its potential for explaining variation. That is, not everyone is lateralized in the same way. For every generalization about localization of function, an exception can usually be found. Indeed, it is often difficult to make generalizations at all; for example, typical right parietal syndromes do not always occur following right parietal damage, but may occur following damage to other structures (see DeRenzi, 1982). This sort of individual difference is to be expected if the present theory is correct, because the mechanism of differentiation is sensitive to the parameter values used. For example, the precise "transmission time" over the corpus callosum is important for ensuring that modules on the same side as the "target" module are selected over other-sided ones. If transmission is relatively fast, same-sided modules will not be selected as often over input from other-sided modules, and hence will not become as differentially exercised. Interestingly, Witelson (1985) found large variations in the number of fibers in the corpus callosa of different people, with more strongly right-handed people having smaller callosa; this result makes perfect sense if a) more strongly right-handed people are more strongly lateralized, and b) fewer fibers result in slower transmission times--and hence greater probabilities that modules in the same hemisphere as "target" modules will become more exercised. In addition, women have shorter, thicker corpus callosa than men, which may imply faster

transmission times and hence less pronounced lateralization. The usefulness of these sorts of speculations cannot be answered without a fully functioning computer simulation model, which is currently being developed in our laboratory.

A virtue of a theory of processing modules is that the theory itself can be modular. That is, we can add to the theory by expanding the number of modules examined, without affecting the portions of the theory previously developed. Indeed, this ability to simply add without having to modify the previously posited modules is one sign that the earlier theory is correct, that the actual modules have been characterized. This modular property is fortunate, given the ultimate goals of the present theory. The theory ultimately should allow us to account for all of the major findings on visual hemisphericity (e.g., see Kinsbourne and Hiscock, 1983; Springer and Deutsch, 1981). In particular, we need a precise account of results like those of Bisiach and Luzzatti (1978) and Bisiach, Luzzatti, and Perani (1979), who found "unilateral visual neglect" in imagery. That is, they found that damage to the right parietal lobe can result in a patient's ignoring the left half of not only what is seen, but what is imaged. This result presumably has something to do with processing of the coordinate spatial relation we have posited, but the precise account is not yet clear. In addition, Newcombe and Russell (1969) found selective deficits in different spatial abilities following right parietal damage, and the deficits depended in part on the precise location of the damage within the parietal lobe itself. The nature of this selective breakdown must be specified by the theory.

A new way of testing a theory like the present one will be to construct

a simulation model, and then to "lesion" it. The effects of disrupting the model in selected ways will constitute precise predictions of behavioral deficits following brain damage. It will also be interesting to do the obverse: To start with a known deficit, and see what sorts of "lesions" are necessary to make the simulation mimic the deficit. If this procedure is successful, it may be that we are on the road to developing a new, more precise diagnostic tool.

Footnotes

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1. The term image is ambiguous, referring both to the experience itself and the internal representation that gives rise to the percept-like experience. This representation is taken to correspond to a particular brain state. In the present theory, the term "image" refers to the internal representation, not the experience itself. We assume that the conscious experience accompanies the "image" brain state (for some unspecified reason), and thus the experience of "having a mental image" can be taken as a hallmark that the underlying "imagery" brain state is present.

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Figure Captions

Figure 1. Examples of the stimuli used by Shepard and Metzler (1971).

Figure 2. Time to rotate images in the picture plane and in depth in the Shepard and Metzler (1971) experiment.

Figure 3. The map that was imaged and later scanned in the experiment by Kosslyn, Ball and Reiser (1978).

Figure 4. Time to scan between pairs of locations on the imaged map in the Kosslyn, Ball and Reiser (1978) experiment.

Figure 5. The ventral and dorsal visual systems.

Figure 6. Top view of a brain, illustrating how input in the left and right visual fields is processed.

Figure 7. Examples of stimuli used in the Kosslyn and Barrett study.

Figure 8. Results of the Kosslyn and Barrett experiment in which subjects judged whether a dot was on or off a blob or whether a dot was near or far from the blob.

Figure 9. Results from the Kosslyn and Barrett experiment in which subjects judged whether an X was to the left or right of an O or whether the X was within an inch of an O.

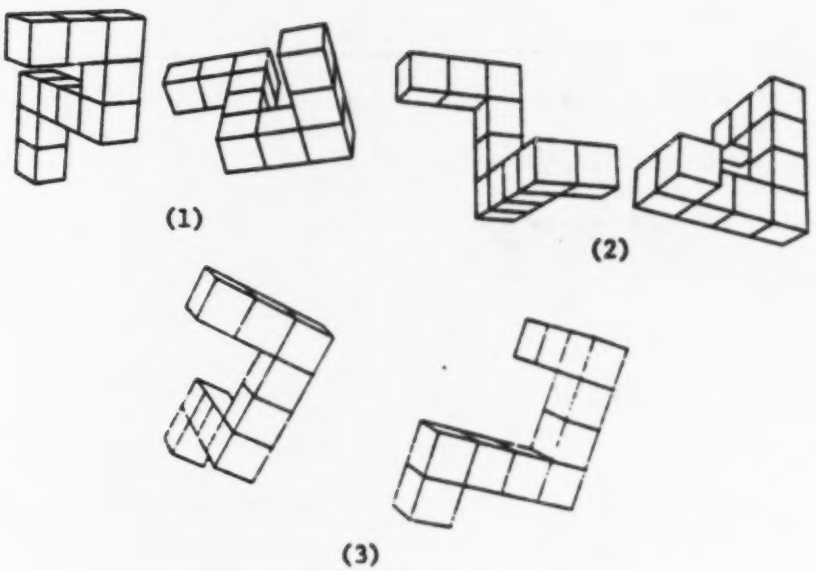


Fig 1

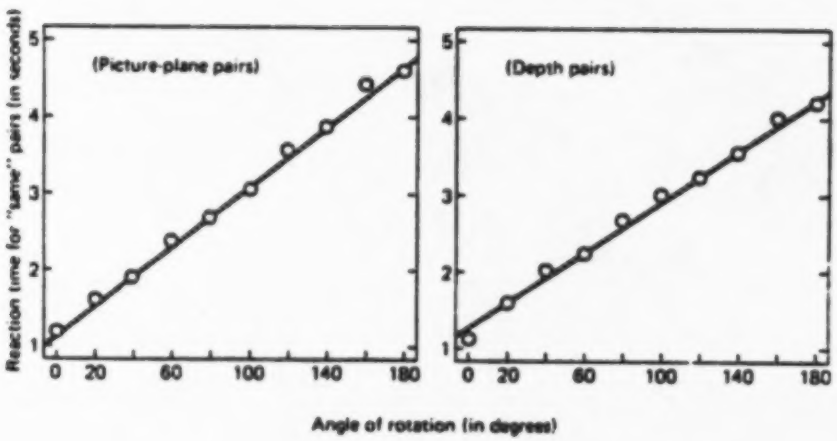

Reaction time for "same" pairs (in seconds)
(Picture-plane pairs)
(Depth pairs)
1
2
3
4
5
0
20
60
100
140
180
Angle of rotation (in degrees)

Fig 2

Fig 3

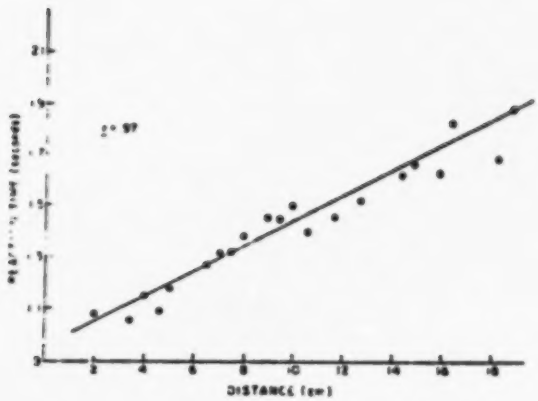


Fig 4

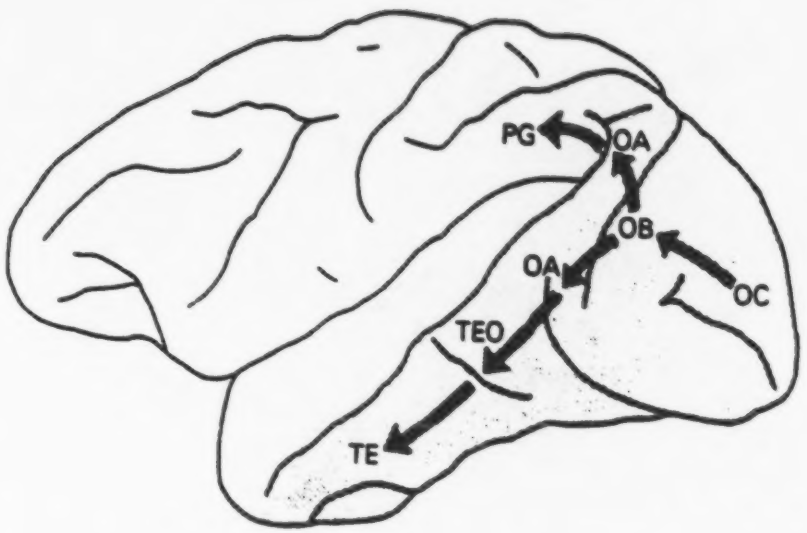


Fig 5

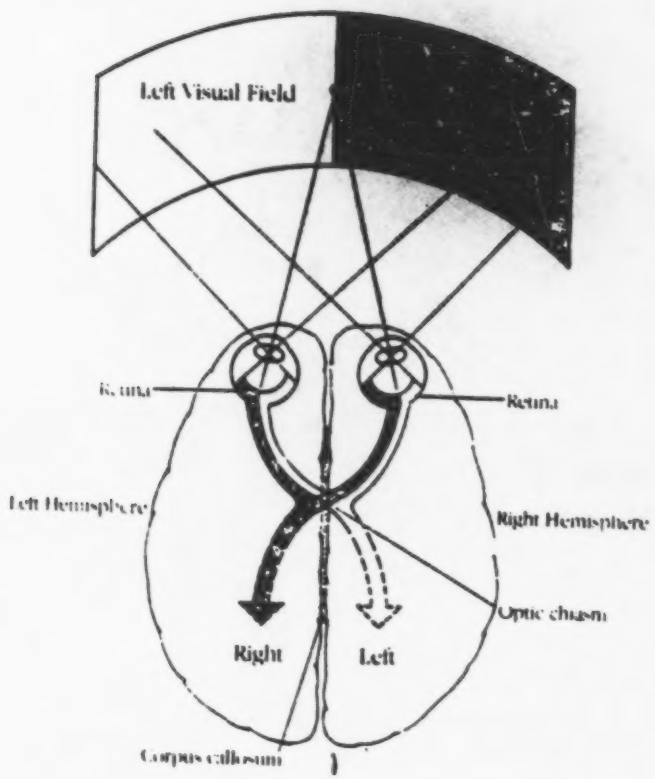


Fig 6

(xeroxed from Springer - Deutch, 1981)

fig 7

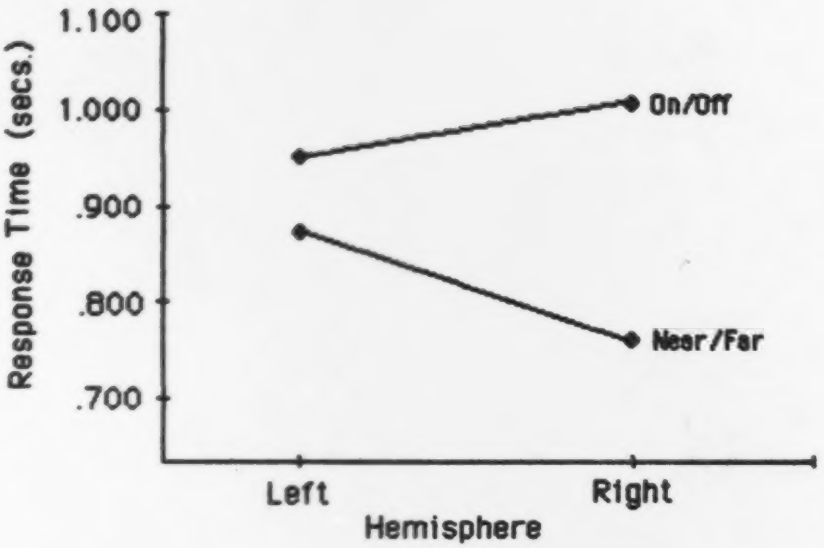
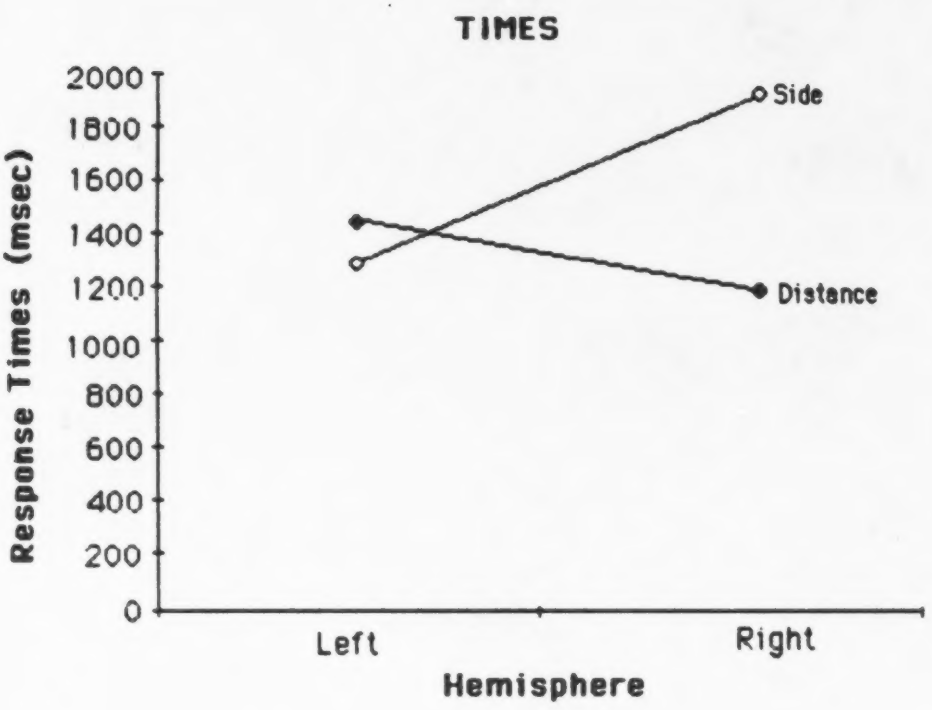
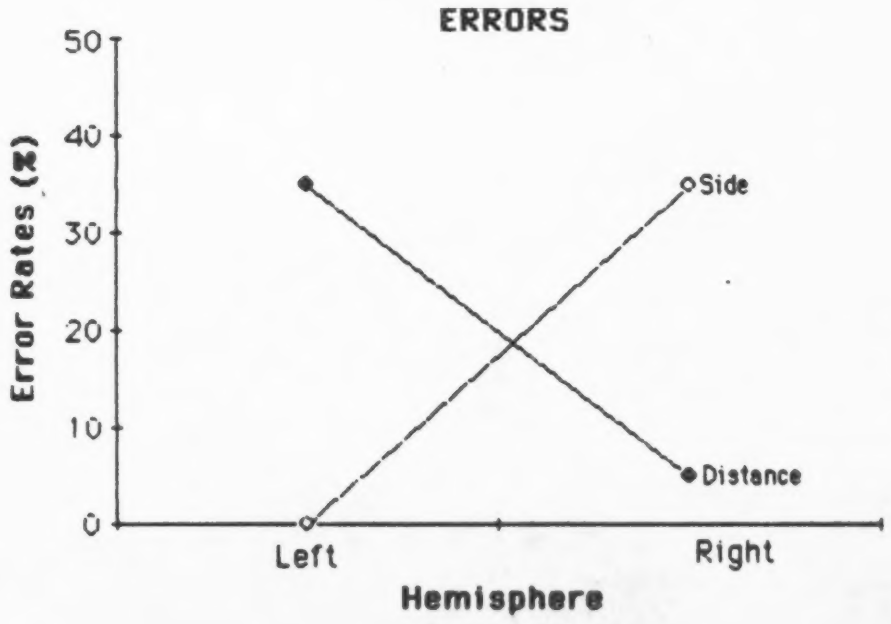
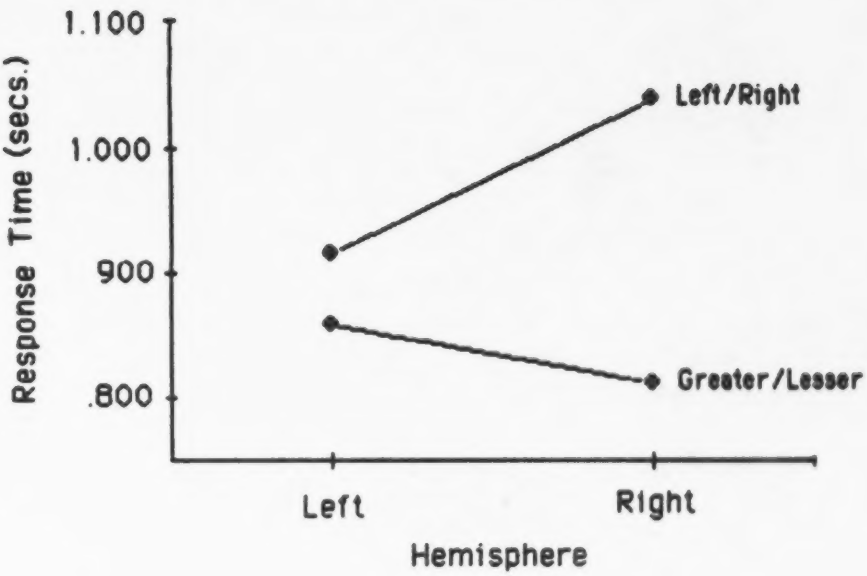

1.100
1.000
.900
.800
.700
Response Time (secs.)
On/Off
Near/Far
Left
Right
Hemisphere

Figure 8


TIMES
Response Times (msec)
2000
1800
1600
1400
1200
1000
800
600
400
200
0
Side
Distance
Left
Right
Hemisphere


ERRORS
Error Rates (%)
50
40
30
20
10
0
Side
Distance
Left
Right
Hemisphere


1.100
1.000
900
.800
Response Time (secs.)
Left/Right
Greater/Lesser
Left
Right
Hemisphere

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